Growth and reproduction of female short-beaked common dolphins, *Delphinus delphis*, in the eastern tropical Pacific

K. Danil and S.J. Chivers

Abstract: We characterize the life-history strategy of female short-beaked common dolphins (*Delphinus delphis* L., 1758) inhabiting the eastern tropical Pacific by estimating several growth and reproductive parameters. Reproductive condition ($n = 700$) and age ($n = 405$) were determined for animals sampled from those incidentally killed in the yellowfin tuna (*Thunnus albacares* (Bonnaterre, 1788)) purse-seine fishery between 1975 and 1993. Females averaged 160.4 cm at age 2 years, 186.5 cm at attainment of sexual maturity, and 197.2 cm at asymptotic length. The estimated age at attainment of sexual maturity was 7.9 years and the oldest animal in the study was 25 years. Calving occurred throughout the year, with females producing a calf approximately every 2.1 years after a gestation period of approximately 11.4 months, an average lactation period of 16.5 months, and an average resting period of 2.8 months. A relatively high percentage (30.4%) of lactating females were simultaneously pregnant, which effectively shortens the average calving interval. No clear evidence of senescence was found. Estimated lengths at birth, 2 years of age, attainment of sexual maturity, and maximum size were greater than those reported for the temperate North Pacific population, indicating that large-scale geographic variation in life history occurs for this species, which likely reflects population-specific adaptations to the tropical and temperate habitats that they occupy.

Résumé : Les estimations de plusieurs variables de croissance et de reproduction nous servent à préciser la stratégie démographique de dauphins communs (*Delphinus delphis* L., 1758) femelles vivant dans le Pacifique oriental tropical. Nous avons déterminé la condition reproductrice ($n = 700$) et l'âge ($n = 405$) chez des animaux échantillonnés parmi ceux qui ont été tués accidentellement au cours des pêches commerciales à la seine coulissante d'albacores à nageoires jaunes (*Thunnus albacares* (Bonnaterre, 1788)) entre 1975 et 1993. Les femelles ont en moyenne une longueur de 160,4 cm à l'âge de 2 ans, de 186,5 cm à la maturité sexuelle et de 197,2 cm à l'asymptote. Nous estimons l'âge de l'atteinte de la maturité sexuelle à 7,9 ans; l'individu le plus âgé de notre étude avait 25 ans. La mise bas se fait pendant toute l'année et les femelles produisent un petit à environ tous les 2,1 années après une période de gestation d'approximativement 11,4 mois, une durée de l'allaitement moyenne de 16,5 mois et une période de repos moyenne de 2,8 mois. Un pourcentage relativement élevé (30,4 %) de femelles nourricières sont en même temps enceintes, ce qui réduit effectivement l'intervalle moyen entre les mises bas. Il n'y a pas d'indication claire de sénescence. Les longueurs estimées à la naissance, à l'âge de 2 ans, à l'atteinte de la maturité sexuelle et à la taille maximale sont supérieures à celles signalées chez la population du Pacifique nord tempéré; il y a donc une variation géographique à grande échelle dans le cycle biologique de cette espèce qui est vraisemblablement le reflet d'adaptations spécifiques à la population aux habitats tropicaux ou tempérés qu'elle colonise.

[Traduit par la Rédaction]

Introduction

Cetacean life-history studies enable us to better understand the basic biology of a species, its relationship to the environment (Börjesson and Read 2003; Danil and Chivers 2006), stock structure (Perrin et al. 1985; Dizon et al. 1994), behavior (Whitehead and Mann 2000), mating systems (Murphy et al. 2005), and anthropogenic effects (e.g., incidental fishery mortality, contaminants, etc.) (Chivers and Myrick 1993; Wells et al. 2005). Although the short-beaked common dolphin (*Delphinus delphis* L., 1758) is

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one of the most abundant cetaceans in the eastern tropical Pacific (ETP) (Wade and Gerrodette 1993), few life-history parameters describing its growth and reproduction characteristics have been published. This study characterizes the life-history strategy of *D. delphis* in the ETP, which will aid in the management of this species impacted by the tuna purse-seine fishery operating in the area.

Short-beaked common dolphins are distributed worldwide in temperate, tropical, and subtropical seas (Fig. 1), and occupy near-shore coastal waters, as well as habitats thousands of miles from shore (Heyning and Perrin 1994). Comprehensive studies on female growth and reproduction of this species have been completed for populations in the North Pacific (Ferrero and Walker 1995), western North Atlantic (Westgate and Read 2007), eastern North Atlantic (Murphy 2004), and the Black Sea (Tomlin 1957) (Fig. 1). In reviewing these studies, it is evident that population variability in life history exists for this species, and thus it is necessary to

Fig. 1. World distribution of *Delphinus delphis* (common dolphin). Shaded regions indicate the known distribution (Heyning and Perrin 1994); circled areas indicate populations whose life histories have been studied comprehensively; and the square area indicates the general study area for this study.
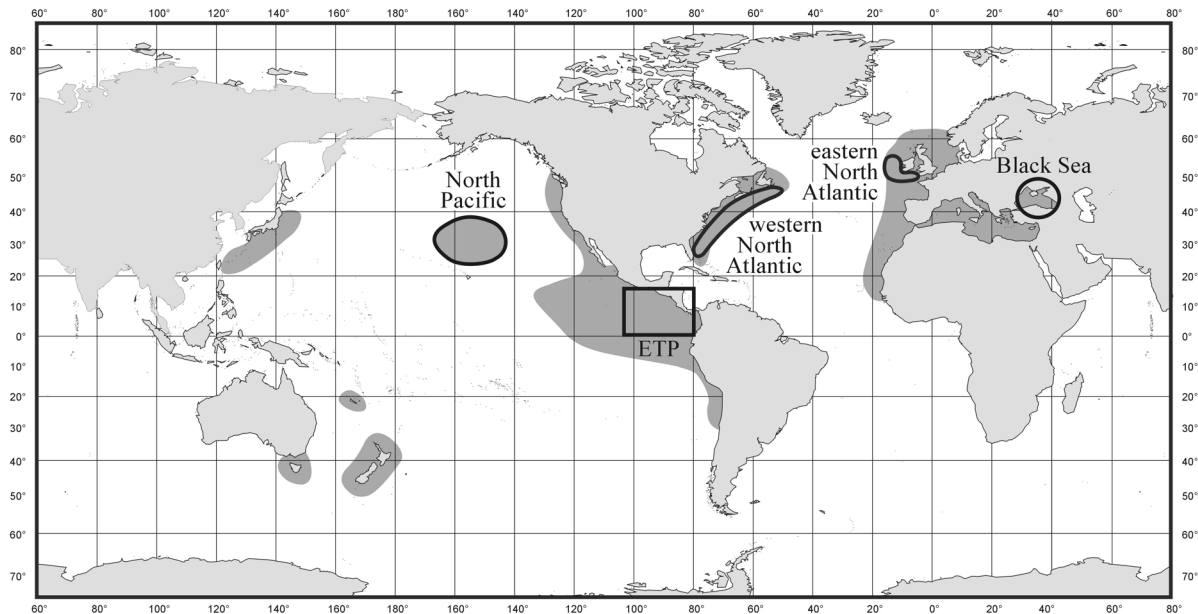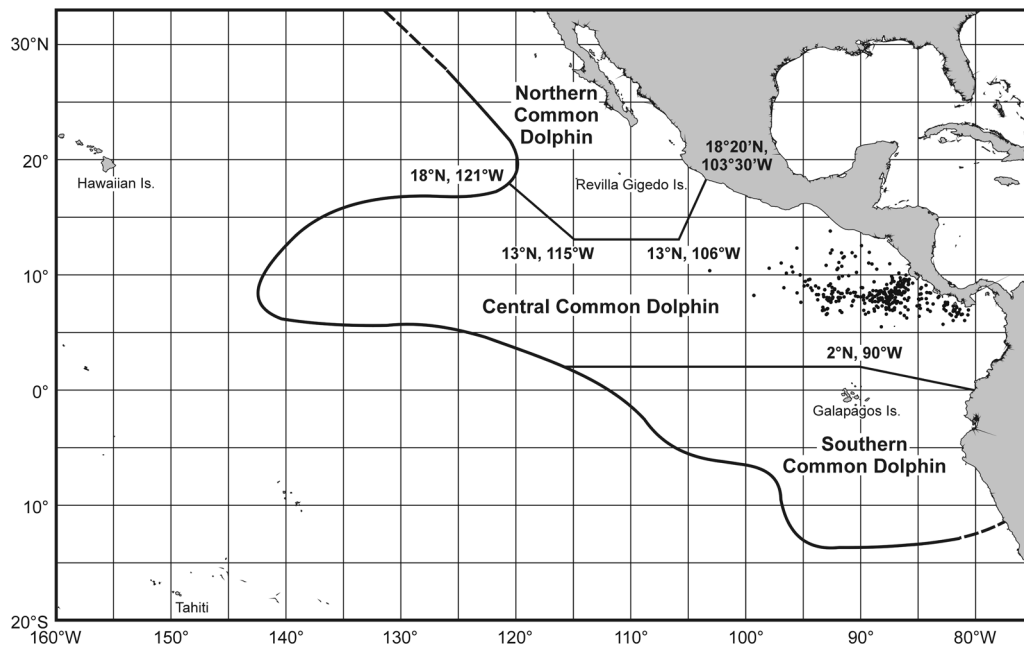

Fig. 2. *Delphinus delphis* (common dolphin) stock boundaries (Perrin et al. 1985) and collection locations of 1108 Central female *D. delphis* samples.

characterize growth and reproduction parameters for the ETP population specifically.

In the ETP, three stocks of *D. delphis* are recognized for management purposes: northern, central, and southern (Fig. 2; Perrin et al. 1985). *Delphinus delphis* stocks in the ETP were defined by hiatuses in distribution, differences in asymptotic length of adult animals, and differences in breeding seasonality, which suggests some degree of reproductive isolation between them (Perrin et al. 1985; Dizon et al. 1994), and therefore they are managed separately. These characteristics also suggest that these stocks have different life histories, therefore, we focused on describing the life-history characteristics of females from the central stock (hereinafter referred to as Central *D. delphis*) for which the greatest number of samples were available. Using data from 1986 to 1990, Wade and Gerrodette (1993) estimated the abundance of Central *D. delphis* to be 406 100 individuals.

In the ETP, research on *D. delphis* has been limited to stock structure, reproductive rates, and timing of reproduction (Henderson et al. 1980; Perrin et al. 1985; Perryman

and Lynn 1993). Prior to the 1985 revision of stock boundaries (Perrin et al. 1985), Henderson et al. (1980) summarized female reproductive phase lengths and pregnancy rates from data collected between 1973 and 1978. Later, using the stock boundaries established in 1985, Perryman and Lynn (1993) described patterns in timing of reproduction and average size of adult animals for all three stocks, using aerial photogrammetry.

Delphinus delphis are impacted by fisheries worldwide (Hobbs and Jones 1993; Evans 1994; Perrin et al. 1994; Tregenza and Collet 1998). In the ETP, incidental mortality of *D. delphis* occurs in the yellowfin tuna (*Thunnus albacares* (Bonnaterre, 1788)) purse-seine fishery. In the late 1950s, the purse-seine fishery began to replace the pole-and-line fishery for tuna in the eastern Pacific Ocean (Perrin 1969; Gerrodette 2002). The new fishery encircled herds of dolphins belonging to the genera *Stenella* Gray, 1866 and *Delphinus* L., 1758, along with the targeted and closely associated schools of yellowfin tuna. *Delphinus delphis* is the third most frequently killed cetacean in this fishery, after pantropical spotted (*Stenella attenuata* (Gray, 1846)) and spinner (*Stenella longirostris* (Gray, 1828)) dolphins (Hall 1998; Bayliff 2002), with a mean of 4551 (range 191 – 12 711) Central *D. delphis* incidentally killed each year between the years 1979 and 1993 (Bayliff 2002). In addition to enumerating the incidental kill of dolphins, technicians collected biological samples from these incidentally killed animals. Using these biological samples, extensive life-history studies on *S. attenuata* and *S. longirostris* were completed (Perrin et al. 1976, 1977). This study, however, is the first comprehensive life-history study of *D. delphis* in the ETP.

In this paper, we describe the life history of female Central *D. delphis* in the ETP using current stock boundaries and all available data to date. In addition to presenting estimates of growth and reproduction parameters, we compare the life-history parameters to those described for this species in the North Pacific (Ferrero and Walker 1995) and to those of other small pelagic dolphins (*S. attenuata* and *S. longirostris*) inhabiting the ETP.

Materials and methods

Specimen and data collection

Scientific observers from the National Marine Fisheries Service (NMFS) and the Inter-American Tropical Tuna Commission (IATTC) collected field and biological data from dolphins incidentally killed in the tuna purse-seine fishery. Specimens were processed using the methods of Perrin et al. (1976). Total body length of animals was measured to the nearest centimetre. Mammaries were examined for the presence of milk, reproductive tracts were collected and preserved in 10% formalin, and teeth were collected from the left lower jaw at midlength. Biological data and tissue samples were only collected from a subset of the observed kill. In the laboratory, ovaries were weighed and examined for the presence of corpora lutea and (or) corpora albicantia. If present, these were then counted and classified as described by Akin et al. (1993). Total corpus count was defined as the number of corpora albicantia and corpora lutea present on both the left and the right ovaries. Females

were considered to be sexually mature if their total corpus count was greater than zero. The reproductive tract was inspected carefully for the presence of a fetus, especially if a corpus luteum was present. Fetuses were sexed, weighed, and measured (Akin et al. 1993).

Aging

Following the protocol of Myrick et al. (1983), teeth were decalcified, cut with a freezing microtome into 25 μm thick longitudinal serial sections, and stained with hematoxylin. Sections were mounted on gelatin-coated slides, and cover slip margins were sealed with DPX mounting medium (Lockyer 1995). Ages were determined by growth layer groups (GLGs) in the dentine (Myrick et al. 1983; Hohn et al. 1989) under a compound light microscope at 40× and 100× magnifications. Each GLG is interpreted as representing 1 year of life based on a calibration study by Gurevich et al. (1980).

Two readers aged each tooth three times, with at least a week between readings. GLG counts were made without reference to specimen information such as total body length, reproductive status, or previous GLG counts. The mean GLG count of the three readings pooled from both readers is referred to as the total pooled mean age estimate, whereas the mean for an individual reader is referred to simply as mean age estimate. Pooled mean age estimates were used as the best estimate of age for each specimen. Coefficient of variation ($CV = (SD/mean) \times 100$) was used to measure the precision of the age estimates (Chang 1982).

Stable age distribution

A simulated expected stable age distribution was generated for comparison with the data using a Leslie matrix population model with 30 age classes. Age-specific fecundity and survival schedules were produced using the reproductive parameter estimates presented in this paper and the methods for estimating survival rates presented by Barlow and Boveng (1991), together with the data from a longitudinal study of bottlenose dolphins, *Tursiops truncatus* (Montagu, 1821) (Wells and Scott 1990), to fit the survival model.

Length and age parameter estimation

Two methods were used to estimate length at birth and age and length at attainment of sexual maturity: (1) the sum-of-fraction-immature method (Hohn 1989) and (2) logistic regression. A third method presented by DeMaster (1978) has been used in many life-history studies in the past, but we determined this method to be inappropriate for our data set because of the need to use predicted rather than true proportions (Laws et al. 1975) for some age classes.

Sum-of-fraction immature method

The sum-of-fraction immature (SOFI) method estimates the average age at attainment of sexual maturity (ASM) as

$$[1] \qquad \text{ASM} = j + \sum_{i=j}^{k} p_i x_i$$

where j is the age of the youngest mature animal, k is the age of the oldest immature animal, p_i is the proportion of immature animals in age class i, and x_i is the number of

age classes combined in age class i. Variance was estimated as

[2] $\quad \text{Var(ASM)} = \sum_{i=j}^{k} \dfrac{p_i(1 - p_i)x_i}{n_i - 1}$

where n_i is the sample size for age class i.

To estimate average length at attainment of sexual maturity (LSM), the SOFI method was modified to use constant length intervals (5 cm) instead of ages so that

[3] $\quad \text{LSM} = j + \sum_{i=i_{\min}}^{i_{\max}} p_i x_i$

where j is the lower limit of the length class with the smallest mature animal, $i_{\min}$ is the length class with the shortest mature animal, $i_{\max}$ is the length class with the longest immature animal, p_i is the proportion of immature animals in length class i, and x_i is the number of age classes combined in age class i. Variance was estimated as

[4] $\quad \text{Var(LSM)} = \sum_{i=i_{\min}}^{i_{\max}} \dfrac{p_i(1 - p_i)x_i}{n_i - 1}$

where n_i is the total number of animals in the ith length class.

The SOFI method was modified similarly to estimate average length at birth, where j is the lower limit of the length class with the smallest calf, $i_{\min}$ is the length class with the smallest calf, $i_{\max}$ is the length class with the longest fetus, p_i is the proportion of fetuses in length class i, x_i is the interval width of length class i, and n_i is the total number of animals in the ith length class.

Logistic regression

Logistic regression analysis, based on maximum likelihood, was used to estimate ASM and LSM by determining the length and age at which 50% of a combined sample of immature and mature animals was predicted to be mature. Similarly, logistic regression was used to determine estimated length at birth (ELB) by determining the length at which 50% of a combined sample of fetuses and postnatal specimens was predicted to be born. All female postnatal specimens, male postnatal specimens ≤98 cm (to fill a gap in the female data, since growth rates of *D. delphis* calves do not vary by sex; Westgate 2005), and fetuses (regardless of gender) with an associated total body length were used in the logistic regression analysis. Confidence intervals were constructed based on 1000 bootstrap replicates conducted by sampling the data with replacement. Alternative estimates of ASM and ELB were compared with observed estimates using 1000 bootstrap replicates to estimate the probability that the difference between original and hypothetical estimates was zero.

To determine whether the calculated mean length at birth is significantly biased by undocumented calf mortality (i.e., missing calves in the data set; Archer et al. 2001), an alternative estimate of length at birth was calculated (using the logistic regression method) based on a hypothetical data set and then compared with the original estimate. The hypothetical data set added 15% more (+9) calves, which is the

upper range of undocumented mortality estimated by Archer et al. (2001), to the smallest indeterminate length class (84 cm).

Comparison of methods

For this study, the preferred method for calculating ASM, LSM, and ELB was the logistic regression followed by the SOFI method. The binning required for the SOFI method likely results in a loss of resolution, and the associated variance appears to be underestimated. The ability to input raw data and to capture the variance of the fit with bootstrap replicate sampling makes the logistic regression method preferable, and it is therefore used in all parameter comparisons in this study.

Gestation

Gestation was estimated using Perrin et al.'s (1977) regression equation

[5] $\quad \log(y) = 0.1659 + 0.4856\log(x)$

where y is the length of gestation and x is the length at birth. This equation is based on the positive correlation between length at birth and gestation of four closely related delphinids. Gestation could not be estimated using the method of Hugget and Widdas (1951) because the available data violated the assumption that reproduction is seasonal.

Growth

Using the Laird–Gompertz formula (Laird 1969), a two-phase growth model (Perrin et al. 1976, 1977) was used to simultaneously fit separate equations to female age at length data, using an iterative least-squares method. This two-phase model was used to account for the secondary growth spurt observed in small delphinids (Perrin et al. 1976, 1977). The Laird–Gompertz model is

[6] $\quad L(t) = L_0 e^{(a/\alpha(1 - e^{(-\alpha t)}))}$

where $L(t)$ is length at time t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth. The first model was anchored at the ELB. The intersection point of the two models was estimated as the age at which the total sum of squares for the fit of both models was smallest.

Seasonality

Birth dates for animals estimated to be <1 year old (i.e., total length ≤135 cm) were back-calculated using

[7] $\quad d_b = d_c - 30\dfrac{l_c - l_b}{r}$

where d_b is the day of the year of the birth date, d_c is the day of the year of collection, l_c is the length at collection, l_b is length at birth, and r is growth rate in centimetres per month. The ELB derived from the logistic method was used as an estimate of l_b. The growth rate of 4.0 cm/month obtained from the previously described growth model was used as the estimate for r.

Reproductive phases and calving interval

Previous workers have estimated dolphin calving interval

Table 1. Reproductive condition of 333 sexually mature female *Delphinus delphis* collected between 1975 and 1993.

Condition	n	Percentage
Pregnant only (P)	83	24.9
Lactating only (L)	149	44.8
Pregnant and lactating (PL)	65	19.5
Resting	36	10.8
Total sexually mature females	333	

Fig. 3. Total body length frequency distribution of Central female *D. delphis* sampled ($n = 1108$). The *x*-axis labels represent the upper bound of the length interval.
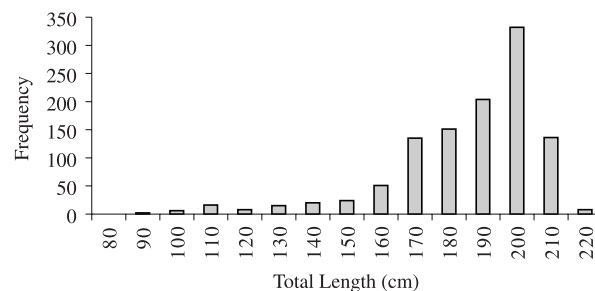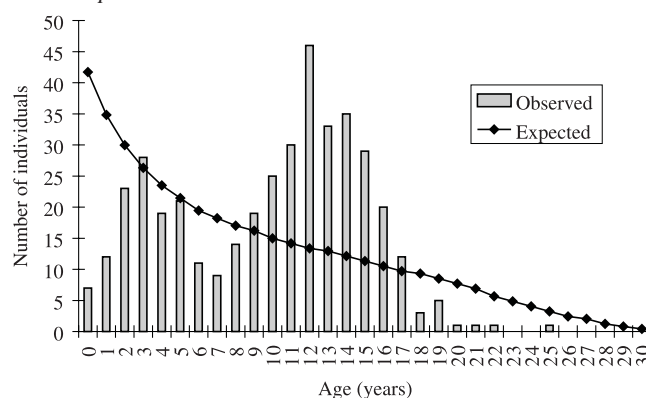

Fig. 4. Age frequency distribution of sampled Central female *D. delphis* ($n = 405$) and predicted stable age distribution for Central *D. delphis*.

based on the proportions of pregnant, lactating, and resting females (Perrin et al. 1976). This approach is flawed, as it equates pregnancy rate with birth rate, ignoring fetal mortality (Perrin et al. 2003). However, it does yield a minimum estimate, which is an underestimate to the extent that pregnancy rate overestimates birth rate and is used thusly here.

The proportion of pregnant, lactating, and resting (those neither pregnant or lactating) females (Table 1) was used in combination with the gestation period to determine estimates of the calving interval (Perrin et al. 1976). The summation method (gestation + lactation + resting phases) and the reciprocal of the annual pregnancy rate (APR) were used to calculate two estimates of calving interval (Perrin et al. 1976). The equations for estimating time spent lactating and resting, as well as APR, are

$$[8] \quad \text{Lactation} = \frac{L}{P} \times G$$

$$[9] \quad \text{Resting} = \frac{R}{P} \times G$$

$$[10] \quad \text{APR} = \frac{P}{G}$$

where L is the proportion of sexually mature females lactating (including those simultaneously pregnant), P is the proportion of sexually mature females pregnant (including those simultaneously lactating), G is the length of gestation in years, and R is the proportion of sexually mature females neither pregnant nor lactating.

Results

The sample

Total body length, collection date, and collection location were recorded for 1108 female Central *D. delphis* collected between 1975 and 1993 (Fig. 2). Samples were collected in each year, except 1984, with the majority of specimens being collected in the 1970s and late 1980s. Reproductive status was determined for 700 of these specimens, of which 405 were randomly subsampled for age determination. Although specimens were also available for the years 1973 and 1974, these were omitted from the analyses to reduce the likelihood of including animals from adjacent stocks (Danil and Chivers 2006). Specimens were collected during every month of the year, with the majority of sampling occurring between April and August.

To assess potential subsampling biases of the aged and reproductive samples, the length frequency distributions of these subsamples were compared with that of the total sample. A two-sample Kolmogorov–Smirnov test demonstrated that there was no significant difference ($P = 0.731$) between the reproductive subsample and the total sample, but a significant difference ($P = 0.004$) between the aged subsample and the total sample. However, there is no significant difference ($P = 0.111$) if the length frequency distributions of the aged and total samples are compared using only lengths within the range of sexually mature females, and therefore reproductive estimates associated with age are not likely biased by subsampling.

Length and age of female *D. delphis* ranged 84–213 cm (Fig. 3) and 0–25 years (Fig. 4), respectively. The age distribution was bimodal with peaks in the age classes of juveniles (i.e., 2–5 year olds) and sexually mature adults (i.e., 11–15 year olds). This is quite different from what is expected under a stable age distribution. The greatest frequency is expected for neonates, followed in order by yearlings, juveniles, and adults (Fig. 4).

Aging

The calculated CVs for reader 1, reader 2, and the pooled mean age estimate were 17.0%, 14.0%, and 19.3%, respectively. A Spearman's rank correlation test for each reader indicates that there was no relationship between CV and mean age estimate (reader 1: $P = 0.741$; reader 2: $P = 0.271$). Between readers, 47% of readings agreed to within 1 year and 70% of readings agreed to within 2 years. Mean age esti-

Fig. 5. A logistic curve fitted to length and postnatal status of Central *D. delphis*. The length at which 50% of specimens are predicted to be calves is 87.0 cm (95% CI, 84.6–89.2 cm), which is the estimated length at birth. The circles represent individual samples and the range of the *x* axis is limited for presentation.
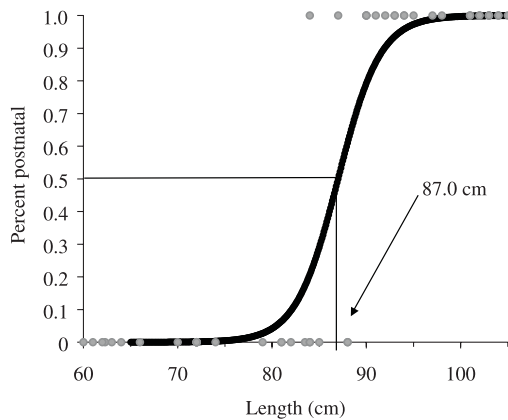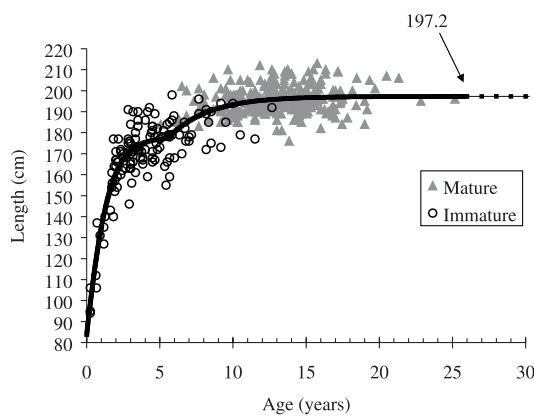

Fig. 6. Two-phase Laird–Gompertz growth model fitted to age-at-length data of female *D. delphis*. The predicted asymptotic length from the model is 197.2 cm

mates were not significantly different between readers (Wilcoxon signed-rank test: $z = -0.857$, $P = 0.392$).

Parameter estimation

Length at birth

The smallest calf was 84 cm long and the largest fetus was 88 cm long. Using logistic regression (Fig. 5) and a modified SOFI method based on 5 cm groupings, ELBs were 87.0 cm (95% CI, 84.0–89.0) and 88.0 cm (SE = 0.141), respectively. The alternative ELB, which accounts for undocumented calf mortality, was estimated to be 83.7 cm (95% CI, 81.6–85.9) and is significantly different ($P = 0.029$) from the original ELB based on logistic regression.
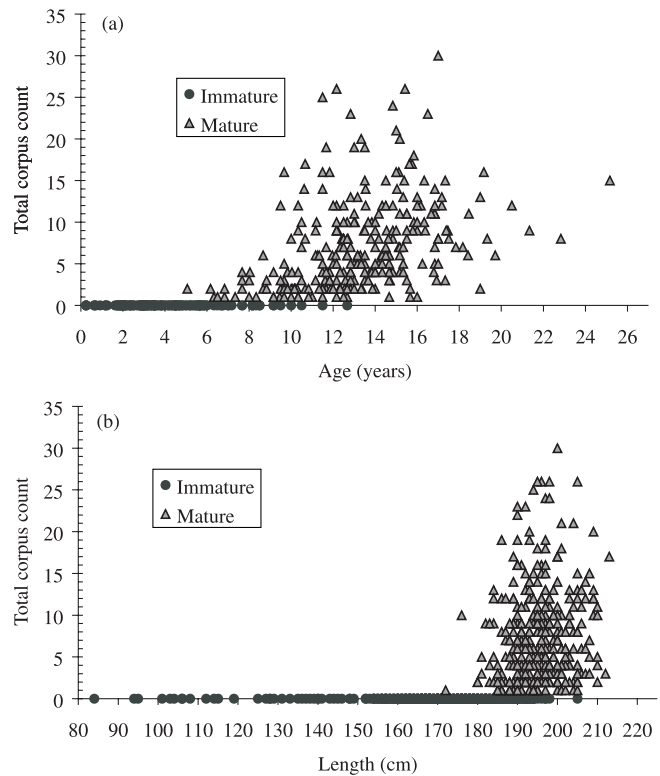
Gestation

Using the ELB of 87.0 cm, gestation was estimated to be 11.4 months. This approximation of gestation is used in calculating reproductive phases.

Postnatal growth

The equation for the first phase of growth was

Fig. 7. Scatterplot of total corpus count of Central female *D. delphis* as a function of (*a*) age ($n = 405$) and (*b*) length ($n = 700$).

$$[11] \qquad L(t) = 87.0e^{(0.687/0.958(1-e^{(-0.958t)}))}$$

where $L(t)$ is length at time t and t is the age. For the second phase, the growth equation was

$$[12] \qquad L(t) = 177.4e^{(0.041/0.386(1-e^{(-0.386t)}))}$$

Growth was rapid through age 2 with predicted lengths of 1 and 2 year olds being 135.4 and 160.4 cm, respectively. After age 2, growth slowed until age 5.6, where it increased again. Growth subsequently slowed again until it reached an asymptote at 197.2 cm (Fig. 6).

Age and length at attainment of sexual maturity

The youngest sexually mature female was 5 years old and the oldest sexually immature female was 12 years old (Fig. 7*a*). The average ASM was estimated to be 7.8 years (SE = 0.020) using the SOFI method and 7.9 years (95% CI, 7.3–8.3) using the logistic method (Fig. 8).

If juveniles are indeed "missing" and prime females are in "excess", as the comparison of a stable age distribution to that of this study suggests (Fig. 4), the calculated average ASM may be incorrect. To investigate this, ASM was calculated for two hypothetical populations, A and B. In both populations, "missing" animals from the stable age distribution (Fig. 4) were included and "excess" animals excluded. In population A, the proportion of mature individuals in each age class was assumed to be the same as observed in our sample. In population B, all "missing" animals <9 years were assumed to be immature animals (schooling elsewhere according to maturity status and thus not sampled), with the remaining age classes matching observed proportions in the

Fig. 8. A logistic curve fitted to age and maturity status of Central female *D. delphis*. The length at which 50% of specimens are predicted to be mature is 7.9 years (95% CI, 7.3–8.3 years), which is the estimated ASM. The circles represent individual samples.
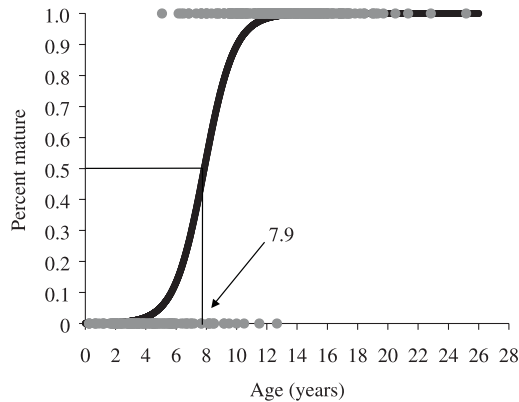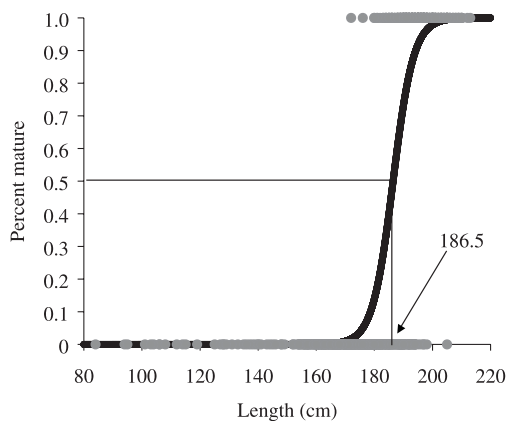

Fig. 10. Mean number of corpus scars increases with age in Central *D. delphis*. The points represent means for 1 year age classes of sexually mature individuals. Vertical bars represent SE of the mean count for each age class.
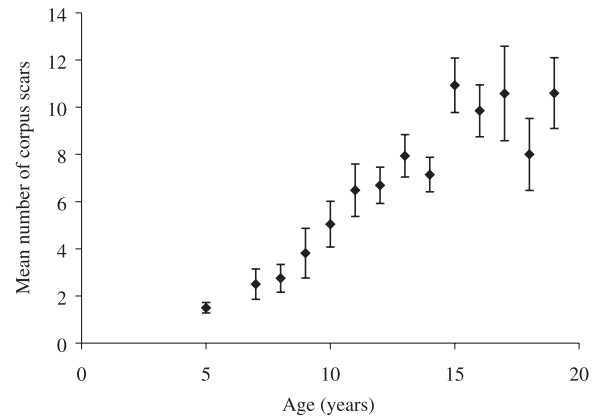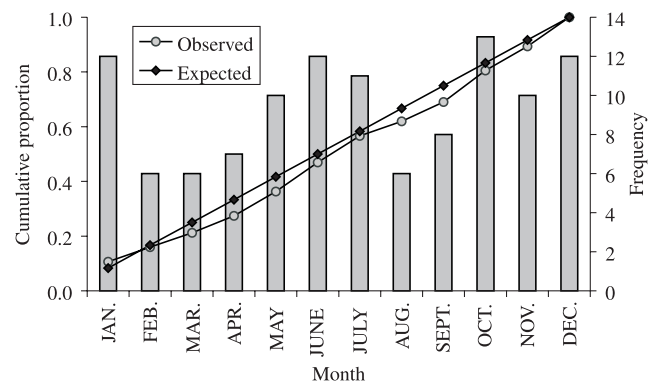

Fig. 9. A logistic curve fitted to length and maturity status of Central female *D. delphis*. The length at which 50% of specimens are predicted to be mature is 186.5 cm (95% CI, 185.5–187.4 cm), which is the estimated LSM. The circles represent individual samples.

Fig. 11. Distribution of cumulative back-projected birth dates of Central *D. delphis*. The observed cumulative distribution is not significantly different from an expected uniform cumulative distribution ($P > 0.10$), indicating no seasonality in female reproduction. Bars indicate frequency of back-calculated birth dates of female ($n = 56$) and male ($n = 57$) *D. delphis* that are ≤135 cm.

sample. The ASMs for populations A and B were calculated to be 7.6 years (95% CI, 7.1–8.0) and 8.0 years (95% CI, 7.6–8.5), respectively. Neither population A ($P = 0.199$) nor population B ($P = 0.697$) differed significantly from the observed ASM.

Sexually mature females ranged 172–213 cm long (Fig. 7*b*) and averaged 195.4 cm long (SE = 0.351, $n = 351$). The largest sexually immature female was 205 cm long (Fig. 7*b*). Using the modified SOFI method and the logistic method (Fig. 9), average lengths at sexual maturity were estimated to be 187.0 cm (SE = 0.010) and 186.5 cm (95% CI, 185.5–187.4), respectively.

Ovulation
Total corpus counts in sexually mature females ranged 1–30. Spearman's rank correlation test of mean number of corpus scars on age class showed a significant increase in corpus scars with age ($r_S = 0.938$, $P < 0.001$; Fig. 10). Corpus counts for the youngest and oldest age classes were combined with the adjacent age class so that sample sizes were greater than five for the 5 and 20 year age classes. Among

mature females, the mean number of corpus scars was greater in the left ovary than in the right ovary (Wilcoxon signed-rank test: $z = -20.222$, $P < 0.001$). In fact, at least 92% of the first four ovulations occurred in the left ovary. This asymmetric ovarian activity corresponds with the observation that 93% of pregnancies occurred in the left uterine horn. A gradual shift to using both ovaries occurs with increasing corpora. This shift is pronounced after 14–15 corpora have accumulated, with 50% of females having corpora in both ovaries.

Reproductive seasonality
No peaks in birth dates were identified in the distribution of back-calculated birth dates (Fig. 11). The Kuiper's test demonstrated that birth dates were not significantly different ($K = 0.7$, $P > 0.10$) from a uniform distribution (Fig. 11), indicating no seasonality in female reproduction. These results agreed with those found by Perryman and Lynn's (1993) photogrammetry study of Central *D. delphis*.

Reproductive phases and calving interval
The summation of the gestation (11.4 months), lactation

Fig. 12. The proportion of female *D. delphis* that were pregnant and lactating versus age. The proportion of pregnant females decreases with age, along with a concomitant increase in the proportion of lactating females. Vertical broken lines represent how data were binned to calculate proportions, with sample sizes in parentheses.
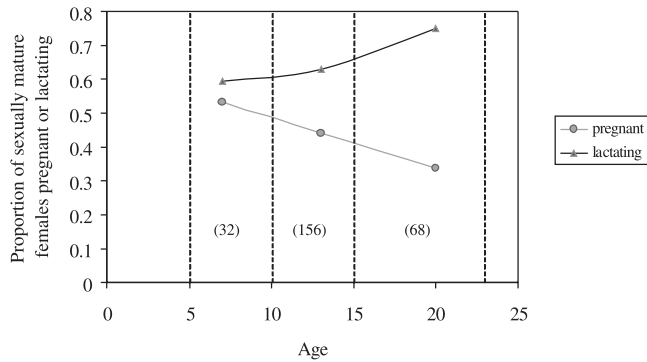
(16.5 months), and resting (2.8 months) phases estimated a calving interval of 30.7 months, or 2.6 years. The second estimate of 25.7 months, or 2.14 years, was derived from the reciprocal of the APR (1/0.468). These are underestimates of calving interval (see sections Materials and methods and Discussion). Of the lactating females, 30.4% were simultaneously pregnant. The data set showed that pregnancy and lactation rates changed with age. That is, pregnancy rate decreased with increasing age as lactation rates increased (Fig. 12).

Postreproductive females

Following the criteria of Perrin et al. (1977), 333 sexually mature females were examined for evidence of senescence. The five criteria indicative of senescence are (1) neither pregnant or lactating, (2) ≥10 corpora, (3) ovaries weigh <3.5 g, (4) no developing follicles, (5) no type 1 or 2 corpora albicantia. None of the 333 animals showed clear evidence of being post reproductive, since none met all five criteria. Seven specimens have met at least three of the five criteria (the first two criteria plus one of the last three criteria), and two specimens have met the first four criteria.

Discussion

The sample

The opportunistic nature of sampling carcasses for life-history studies limits our understanding to the portion of the population sampled, without the knowledge of how well this represents the entire population. In addition, opportunistic sampling often restricts the type of analyses performed because of small sample sizes. However, the long-term data collection effort and relatively high incidental kill in the ETP resulted in a large sample size (e.g., $n = 400$ for individuals with age and reproductive status) for this study. Thus, we were able to estimate most parameters with certainty and to conduct analyses not possible with a more limited data set. For example, Ferrero and Walker (1995) considered many of their estimates provisional, since their data set consisted of only 59 females with age and reproductive data. Similarly, two recent studies on *D. delphis* had

<65 females with age and reproductive status (Murphy 2004; Westgate and Read 2007).

Age

The age distribution of the sample is markedly different from that of female *Stenella longirostris orientalis* Perrin, 1990 (Chivers 2002) and more similar to that of female *S. attenuata* (Barlow and Hohn 1984) that inhabit the same area and are impacted by the same fishery. That is, both calves and juveniles are underrepresented and reproductively prime individuals are overrepresented in the age distribution (Fig. 4) when compared with an expected stable age distribution. Several alternative explanations for the age distribution in *S. attenuata* were outlined by Barlow and Hohn (1984), which included (*i*) school segregation, (*ii*) a variable rate of tooth deposition, and (*iii*) nonstable age distribution that reflects a large perturbation in the population.

If schools are segregated by age or reproductive class, juvenile animals may inhabit different areas, or they may not join herds that are associated with tuna, which are targeted by the purse-seine fishery. Conversely, females in their prime reproductive years appear to be strongly associated and impacted by the purse-seine fishery compared with all other age classes. Kleinenberg (1956) and Tomlin (1957) documented herd segregation of *D. delphis* in the Black Sea, where females predominantly occur offshore during periods of calving and early lactation. Population segregation has also been suggested for the North Pacific population of *D. delphis* (Ferrero and Walker 1995) to explain the paucity of pregnant females and neonates in their sample collected from a high-seas drift-net fishery. In addition, Westgate and Read (2007) suggested that gender-based habitat partitioning or herd segregation may have accounted for the significant sex bias seen in western North Atlantic *D. delphis* samples.

Variable tooth rate deposition may lead to misinterpretations of growth layers, leading to inaccurate estimates of ages. Since the age distribution of *D. delphis* in the North Pacific (Ferrero and Walker 1995) is quite different from that found in the ETP (Fig. 4), variable tooth rate deposition for this species seems a less likely hypothesis. The difference may reflect inherent sampling biases of the two fisheries. However, it is conceivable that tooth rate deposition could vary within a species in response to habitat or prey differences and therefore could still be an explanation. Exploring this explanation further is complicated because there are likely other biases or inaccuracies in reading GLGs in the teeth.

Incidental mortality in the purse-seine fishery certainly has resulted in perturbation in the population, with Central *D. delphis* mortality peaking at 22 808 in 1961 (Smith 1979). However, the population has been considered stable since the early 1980s (Anganuzzi and Buckland 1994). Considering the evidence for segregation in other *D. delphis* populations, this may be the more likely explanation for the observed age distribution than a nonstable age distribution in the population. The "dip" in animals <2 years old may also be a sampling artifact, partially explained by limited sampling of these age classes by observers and by calves that were initially present in the school but were not caught in the purse-seine net (Archer et al. 2001). The skewed age

Table 2. Comparison of parameter estimates using the original and hypothetical estimated lengths at birth (ELBs) for Central female *D. delphis*.

	Original	Hypothetical
Gestation (month)	11.4	11.2
Lactation period (month)	16.5	16.2
Resting period (month)	2.8	2.7
Growth rate during the 1st year (cm/month)	4.0	4.3
Length at 1 year (cm)	135.4	134.7
Length at 2 years (cm)	160.5	160.4
Asymptotic length (cm)	197.2	197.2
Time of birth	—	Shifts to 1 month earlier for some specimens
Seasonality	None	None
Annual pregnancy rate (APR)	0.47	0.48
Calving interval (1/APR; month)	25.7	25.2

distribution (compared with a stable age distribution) is likely an artifact of selectivity and vulnerability issues associated with the fishery.

Length at birth

Although the alternative ELB (83.7 cm) was significantly different than the primary ELB (87.0 cm) from our data set, it is important to remember that this is an "extreme" estimate with all new calves added to the hypothetical data set being of the smallest length class observed. Even with this "extreme" alternative estimate, growth and reproductive parameters associated with this estimate did not change to an extent that would affect the management or our understanding of this species (Table 2).

Sexual maturation

Our estimated mean length of sexually mature females (195.4 cm) is not statistically distinguishable from previous mean adult length estimates of 194.3 cm (Student's t test: $P = 0.33$) by Perrin et al. (1985) and 194.8 cm (Student's t test: $P = 0.27$) by Perryman and Lynn (1993) for Central female *D. delphis*. Similarly, the estimated ASM is not significantly different from the alternative estimates of ASM, and thus the apparently skewed age distribution of our sample does not likely impact our estimation of ASM to a degree that would affect population models of Central female *D. delphis*.

Ovulation

The wide scatter in the plot of corpora versus age for all individuals (Fig. 7a) demonstrates the individual variation in ovulation rates that has also been documented in studies of other species (Perrin et al. 1976, 1977; Myrick et al. 1986). Corpus scars increase with age (Fig. 10). This indicates that these structures persist to some degree through time and may offer insight into an individual's reproductive history. However, the relevancy of this reproductive history is dependent on further research to determine whether corpora albicantia represent scars of ovulation or pregnancy.

The asymmetry of corpora scars in each ovary indicates that there is a prevalence of activity in the left ovary (93% of pregnancies occurred in the left uterine horn), similar to what has been seen in other delphinids (Perrin et al. 1976, 1977; Murphy 2004).

Reproductive phases and calving interval

Although the estimated gestation of 11.4 months is an approximation, it is well within the range (10–12 months, with most estimates being between 11 and 12 months) of what has been estimated for other *D. delphis* populations (Tomlin 1957; Harrison et al. 1972; Hui 1979a; Henderson et al. 1980; Ferrero and Walker 1995; Sterba et al. 2000; Murphy 2004; Westgate and Read 2007). Our estimate of gestation is comparable with the 11.7 months estimated by Westgate and Read (2007), which we consider to be the best estimate to date (estimated using the method of Hugget and Widdas (1951) with the largest sample size), and therefore feel confident in using our estimate to calculate reproductive phases. The calving interval estimated from the sum of reproductive phases (2.6 years) is likely longer than that estimated by the reciprocal of APR (2.14 years) because it sums each reproductive phase separately and does not account for the observed capability of females to be in two phases at once (i.e., simultaneously pregnant and lactating), which effectively shortens the calving interval. Thus, the sum of phases in the calving interval is likely an overestimate for Central *D. delphis* compared with the reciprocal of APR because of the high percentage (30.4%) of lactating females that are simultaneously pregnant.

However, estimates of calving interval overall are minimum estimates because some fetuses die before they are born and some calves die before they are weaned. Therefore, pregnancy rate does not equal birth rate. If Central *D. delphis* experience high fetal mortality rates similar to those in other ETP dolphins (Perrin et al. 2003), the observed proportion of pregnant females is higher than the number of calves produced. The females are effectively pregnant longer per birth, experiencing multiple re-impregnations following miscarriages. Similarly, if there are high calf mortality rates, then more females would be pregnant and the effective calving interval would be longer. Some fetal and calf mortalities certainly exist, and the calculated calving interval is underestimated to some extent. Perrin et al. (2003) incorporated fetal mortality estimates to adjust the average calving interval of *S. attenuata* and *S. longirostris* from 3 to 5 years, and if a similar fetal mortality rate occurs in *D. delphis*, the calving interval could be, on average, 1.7 times longer than reported here. However, if high rates of fetal mortality are a result of fishery interactions, the underesti-

mate of calving interval may be less for *D. delphis* because it is less impacted by the tuna purse-seine fishery (Bayliff 2002) than the two *Stenella* species used in the fetal mortality study.

The observation that pregnancy rate decreases and length of lactation increases with age (Fig. 12) suggests that either younger females wean their calves earlier or are less successful at rearing their calves, and thus become pregnant more often than older females.

Comparison with North Pacific population

Central *D. delphis* differ markedly in size from their conspecifics in the North Pacific. They are significantly longer at birth (87.0 vs. 82.0 cm; one-sample Student's *t* test: $0.02 < P < 0.05$), age 2 (160.4 vs. 146.4 cm), LSM (187.0 vs. 170.7 cm), and mean maximum adult size (196.5 vs. 179.8 cm) (Student's *t* test: $P < 0.001$ for the last three comparisons). To compare maximum adult size to those in the North Pacific study by Ferrero and Walker (1995), we calculated the average total body length of specimens >16 years as they described. They did not report an asymptotic length predicted by a continuous growth curve. Average ASM was comparable between the two populations, indicating that Central *D. delphis* grew faster, having to reach a greater size in the same amount of time. These observed differences, in combination with length differences in adult size noted within the ETP (Perrin et al. 1985; Perryman and Lynn 1993), provide evidence of geographic variation in this species in the Pacific, with longer individuals found in the tropics. Perhaps the productive upwelling-modified waters of the central region (Au and Perryman 1985) provide a stable rich prey source that allows *D. delphis* to reach a greater size. Another explanation may be that longer individuals have evolved in the tropics to dissipate heat more effectively with a higher surface area to volume ratio, as predicted by Allen's rule.

The two-phase growth curve shows a marked secondary growth spurt for Central *D. delphis* females, which is also evident in *S. longirostris* and *S. attenuata* and in the North Pacific *D. delphis* (Perrin et al. 1976; Perrin et al. 1977; Ferrero and Walker 1995). Growth presumably slows after weaning as the calf learns to forage on its own, increases in preparation to attain a sufficient size for reproductive maturity, and slows again as resources are put into reproductive activities and the animal nears asymptotic length.

Comparison with other delphinids in the ETP

Stenella longirostris orientalis, whitebelly spinners (a form of *Stenella longirostris longirostris* (Gray, 1828)), and the northeastern stock of *S. attenuata* inhabit the same general geographic area as Central *D. delphis*. Of these three closely related species, *D. delphis* appear to be most similar to *S. attenuata* in life-history parameters associated with length: ELB, LSM, and asymptotic length (Table 3). However, Central *D. delphis* reached sexual maturity at a significantly earlier age (one-sample Student's *t* test: $P < 0.0001$) and had a calving interval that was shorter than that of northeastern *S. attenuata*. These differences in part reflect differences in longevity between the two species: *S. attenuata* (38 years; Myrick et al. 1986) live longer than *D. delphis* (25 years). *Stenella attenuata* also grew slower during

their 1st year (3.4 cm/month; Hohn and Hammond 1985) compared with *D. delphis* (4.0 cm/month; this study), and this trend of slower growth (typical of longer lived animals) likely continues, therefore taking them more time to reach sexual maturity.

Unique aspects of Central *D. delphis* life history

Central *D. delphis* have a shorter calving interval than the other ETP small delphinid species previously mentioned, eastern North Atlantic *D. delphis* (Murphy 2004), and possibly western North Atlantic *D. delphis* (Westgate and Read 2007). This may be a unique life-history characteristic of this population that is not related to longevity (longevity of *D. delphis* populations are comparable and longevity of spinners is similar to that of *D. delphis*; Table 3). This shorter calving interval likely results from the greater number of lactating females that are also pregnant: 30.4% vs. 9.3% in *S. attenuata* (Myrick et al. 1986), 2.5% in *S. l. orientalis*, and 5.2% in whitebelly spinners (a form of *S. l. longirostris*) (Henderson et al. 1980). However, there is some evidence available suggesting that this may be a characteristic unique to *D. delphis* in general because high proportions of lactating females that are pregnant were also found in the eastern (42.9%) and western (14.3%) North Atlantic populations (Murphy 2004; Westgate and Read 2007). This evidence should be treated cautiously because they were based on small sample sizes ($n = 7$ for both Atlantic populations). Although the eastern North Atlantic population had a longer calving interval than that estimated in this study (Table 3), this difference may be explained by a higher proportion of resting females and the inclusion of stranded specimens in that study. Stranded individuals are likely unhealthy and unable to sustain a pregnancy, which would result in a lower estimated APR and therefore a longer calving interval.

Possible explanations for the occurrence of more lactating females that are pregnant are (*i*) compensation in reproductive output in response to a reduction in population abundance owing to fishery mortality or (*ii*) better ability to manage the increased energy demands of simultaneous lactation and pregnancy in inhabiting productive upwelling regions (Hui 1979*b*; Au and Perryman 1985; Selzer and Payne 1988; Fiedler and Reilly 1994). The primary upwelling region that dominates the water of Central *D. delphis* is the Costa Rica Dome, which has a distinctly higher plankton biomass than surrounding tropical waters (Fiedler 2002). The productive waters of upwelling regions likely support an abundant prey source of deep scattering layer organisms that *D. delphis* feed on (Osnes-Erie 1999), which is likely a richer food source than that available to *S. longirostris* and *S. attenuata* in the less productive Tropical Surface Water that they inhabit.

Although an increase in simultaneously pregnant and lactating females has been hypothesized as a mechanism to increase reproductive output in response to incidental mortality in *S. attenuata* (Chivers and Myrick 1993), *D. delphis* is the least exploited species out of those impacted by the fishery. Because *D. delphis* population size has been relatively stable since the 1980s (Anganuzzi and Buckland 1994), evidence of a density compensatory response would not necessarily be expected. However, it is possible that this

Table 3. Comparison of life-history parameters between female northern offshore pantropical spotted (*S. attenuata*), eastern spinner (*S. longirostris*), whitebelly spinner (*S. l. longirostris*), and common dolphins (*D. delphis*).

Species	ELB	First year growth (cm/month)	LSM	ASM	Asymptotic length (cm)	Calving	Percentage of lactating females that are pregnant	Calving interval (years; 1/APR)	APR	Maximum reported age (years)
Northern offshore *S. attenuata*	85.4[f]	3.13[f]	181[a]	11.3[g]	190[a]	Spring and fall[e]	9.3[g]	3.03[g]	0.33[g]	38[g]
Eastern *S. longirostris*	77[b]	4.75[b]	164.1[b]	5.5[b]	170.9[b]	March–June[e]	2.5[c]	2.95[c]	0.34[c]	26[j]
S. l. longirostris	75.9[d]	4.3[d]	168.8[d]	7.1[d]	174.9[d]	Spring and fall[e]	5.2[c]	2.8[d]	0.36[d]	23[d]
D. delphis										
North Pacific	82[h]	na	170.7[h]	8[h]	179.4[h]	May–June[h]	na	na	na	27[h]
ETP	87.0[i]	4.0[i]	186.5[i]	7.9[i]	197.2[i]	All year[i]	30.4[i]	2.14[i]	0.47[i]	25[i]
Western North Atlantic	92.7[k]	na	200[l]	8.3[k]	202.2[l]	July[k]	14.3[k]	2 (min)[k]	0.25–0.33[k]	30[k]
Eastern North Atlantic	104.1[m]	na	na	9–10[m]	na	May–Sept.[m]	42.9[m]	3.55[m]	0.28[m]	25[m]

Note: ELB, esitmated length at birth; LSM, length at attainment of sexual maturity; ASM, age at attainment of sexual maturity; APR, annual pregnancy rate.

[a]Perrin et al. (1976).
[b]Perrin et al. (1977).
[c]Henderson et al. (1980).
[d]Perrin and Henderson (1984).
[e]Barlow (1984).
[f]Hohn and Hammond (1985).
[g]Myrick et al. (1986).
[h]Ferrero and Walker (1995).
[i]This study.
[j]Chivers (2002).
[k]Westgate and Read (2007).
[l]Westgate (2005).
[m]Murphy (2004).

type of response could be triggered by undocumented incidental kills of dolphins associated with artisanal fisheries in the ETP, whose mortality rates may be unsustainable (Palacios and Gerrodette 1996). It is also possible that both a shorter calving interval and the ability to be pregnant while lactating may result in a higher intrinsic reproductive rate for Central *D. delphis*. Thus, this characteristic may be a species-specific adaptation to rapid population growth in response to some ecological or evolutionary pressures.

The lack of reproductive seasonality in Central female *D. delphis* is unique, considering that *Stenella* spp. inhabiting the ETP reproduce seasonally (although it is diffuse for some species; Barlow 1984), as do *D. delphis* in the North Pacific (Ferrero and Walker 1995), western North Atlantic (Westgate and Read 2007), eastern North Atlantic (Murphy 2004), and the Black Sea (Tomlin 1957). The difference in seasonality between Central *D. delphis* and the aforementioned *D. delphis* populations may simply demonstrate a latitudinal gradient in reproduction in response to different environments: temperate versus tropical. Perryman and Lynn (1993) also observed differences in reproductive seasonality in their comparison of northern, central, and southern stocks of ETP *D. delphis*. Seasons of high productivity are brief at higher latitudes and more protracted at lower latitudes, therefore for many mammals reproductive timing is highly synchronized in populations at high latitudes and more diffuse in populations at low latitudes (Bronson 1989; Boyd et al. 1999). However, what accounts for the difference between *D. delphis* and the *Stenella* spp. inhabiting the same latitudinal gradient? The distributions of *Stenella* spp. in the ETP are known to change seasonally, while that of *D. delphis* do not (Reilly 1990). This suggests that the upwelling regions inhabited by *D. delphis* may provide an environment which is more stable throughout the year in terms of environmental parameters, food availability, and predation risk — all factors that typically affect movement patterns. Females could exploit this stability and meet the energetic demands of pregnancy and lactation year-round.

Conclusions

Comparisons

Length differences between Central and North Pacific *D. delphis* and the lack of reproductive seasonality in Central *D. delphis* (all other studied populations are seasonal breeders) indicate that large-scale geographic variation in life history occurs for this species. This is likely a reflection of the different tropical and temperate environments that these populations inhabit. Differences between Central female *D. delphis* and *Stenella* spp. inhabiting the same geographic region may reflect species-specific adaptations to different habitats. The upwelling-modified tropical waters in which Central *D. delphis* live sharply contrasts with the surrounding warm, less productive Tropical Surface Water that *S. attenuata* and *S. longirostris* inhabit (Au and Perryman 1985). These observations point to the plasticity of *D. delphis* life history and the likely influence of the environment on it.

Management

Management strategies for populations subject to exploita-

tion often use estimated rates of increase in population size based on life-history parameter estimates. Reilly and Barlow (1986) demonstrated that the delphinid population rates of increase for the four vital rates examined were most sensitive to calving interval and noncalf survival rate, followed by age at first birth, and were insensitive to changes in calf survival rate. If calving interval were increased by 1 year, population rates of increase were shown to decrease by approximately 2 percentage points. Following the logic of this example, rates of increase in Central female *D. delphis* population size would be higher (owing to their shorter calving interval) than in *S. attenuata* and *S. longirostris*, which would enable the Central *D. delphis* population to recover from fishery exploitation (or some other mortality event) more quickly than the *Stenella* spp. Actual expected recovery rates can be modeled using the reproductive parameters, such as calving interval and ASM, estimated in this study, although the warning about the underestimation of calving interval should be heeded.

Acknowledgements

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